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Notes on the origin of extensive endorheic regions in central and northern Mexico, and some implications for paleozoogeography

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ABSTRACT

The recent discovery of a fossil of *Enhydritherium terraenovae* in upper Miocene fluvial deposits in Juchipila (Mexico), nearly 200 km away from the nearest coast, together with other known occurrences of the same species in Florida and California, made possible to envision an alternative to the Panamanian and Polar routes of migration through fluvial systems in Mexico. In order to cross from one ocean to the other, individuals of *E. terraenovae* must have passed the continental divide, which is a physiographic feature that separates surface waters that flow into the Atlantic and Pacific versants.

Two vast endorheic regions, which together span more than 400,000 km^2 in area, currently dominate drainage systems in northern and central Mexico. The endorheic regions are broadly bounded by two mountain ranges and coincide with the arid and semi-arid regions of the Chihuahuan desert. These closed basins are an additional obstacle for migration. However, drainage systems are constantly varying and adjusting to changing conditions imposed by climate, tectonic activity, volcanism, and pronounced asymmetries in topography and rainfall distribution. The migration route across Mexico for *Enhydritherium terraenovae* in the late Miocene ($\geq$6 Ma) could have been facilitated by one or more river captures that inverted the flow direction near the headwaters of a drainage system that debouched either into the Gulf of Mexico or the Pacific coast.

Biologists studying fresh water fish faunas in the southern part of the United States and in northern and central Mexico have documented several living species that occur in both the Rio Grande and in the Mezquital rivers, two drainages that are not presently connected, drain in opposite directions (i.e. towards the Gulf of Mexico and the Gulf of California, respectively) and are separated by the endorheic regions. Furthermore, systematic studies of fresh water fish faunas in the region has numerous examples of endemicity and allopatric speciations that are interpreted as evidence of several events of drainage system rearrangement either by stream capture, beheading, or river diversion or by fragmentation caused by formation of closed basins by faulting, volcanic activity or isostatic rebound in the footwall block of normal faults.

The western boundaries of the extensive endorheic regions in Mexico are controlled mainly by a highland produced by intense felsic volcanism during the Sierra Madre Occidental activity (Eocene – Miocene), and the eastern hydrological divide coincides with mountains associated with the fold and thrust belt produced by the Hidalgoan orogeny in early Cenozoic time. Normal faulting associated with Basin and Range extension formed additional closed basins. Another major factor in the formation of the endorheic regions is the terminal Miocene climate change, which caused runoff reduction and lowered the rivers capacity of erosion.

Opening of the Gulf of California changed the overall slope of rivers draining into the Pacific in northwestern Mexico triggering the capture of rivers formerly confined to the closed basins or draining to the Gulf of Mexico. Quaternary normal faults have been documented a few tens of kilometers from the hydrological divides of the endorheic regions, suggesting that in some regions there is an active tectonic component in their formation.

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The location of the crossing point for the otters is uncertain as the fossil record is scant and investigation on the evolution of drainage systems through time in Mexico is in the early stages. However, it is argued that there is a fair chance that the crossing occurred via the Mezquital river capture near Durango city. Isotopic age of the sediments where the *Enhydritherium terraenovae* fossil was collected, imply that the capture must have occurred in the late Miocene.

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1. Introduction

Otters are carnivorous mammals that live in marine coastal areas and/or in rivers. There are three extant otter species in North America; one is marine (*Enhydra lutris*) and the other two inhabit riparian environments (*Lontra canadensis* and *L. longicaudis)*. Most otters reported in Mexico are L. *longicaudis* and their distribution is mainly in the lowlands close to the Pacific and Gulf of Mexico coasts (Fig. 1B). There are also reports of otters in major rivers and their tributaries, and in mountain streams in the western and southwestern portions of the Sierra Madre Occidental, the Trans Mexican Volcanic Belt and in the mountain regions of southern Mexico. *Lontra canadensis* has been reported mostly in the northern part of the country, at or near the Rio Grande and Colorado rivers. The marine otter used to inhabit Mexico's coast along the northern part of the Baja California peninsula, and now it is restricted to the area around Bahía Sebastián Vizcaíno (Gallo-Reynoso, 1997).

The Neotropical otter L. *longicaudis* is adapted to a diverse set of environments from rocky shorelines, coastal savanna swamps to warm or cool climate rainforests, and it may even be found in perennial rivers that cross arid regions. In Mexico there are reports of otters in streams located as high as 1700 masl and *L. longicaudis* has been found at 4000 masl in Andean regions. Present day Neotropical otters are opportunistic predators that feed mainly on fish, crustaceans, insects, amphibians and mollusks, and occasional small mammals, birds and reptiles; their habitat requirements include riparian cover and abundant den sites (Rheingantz and Trinca, 2015).

There are only three records of fossil otters in Mexico. Arroyo-Cabrales et al. (2013) published a brief summary about two localities (Zacoalco and Tlapacoya) in the Trans Mexican Volcanic Belt where Pleistocene fossil otters have been reported (Fig. 1B). Both fossils were classed as *L. longicaudis*, the Neotropical otter extant in Mexico.

The third record of a fossil otter was recently reported by us (Tseng et al., 2017) and it refers to the discovery of a jaw of *Enhydritherium terraenovae* (Fig. 2) in late Miocene fluvial deposits in Juchipila (Fig. 1B). As it is pointed out by Tseng et al. (op. cit.) the

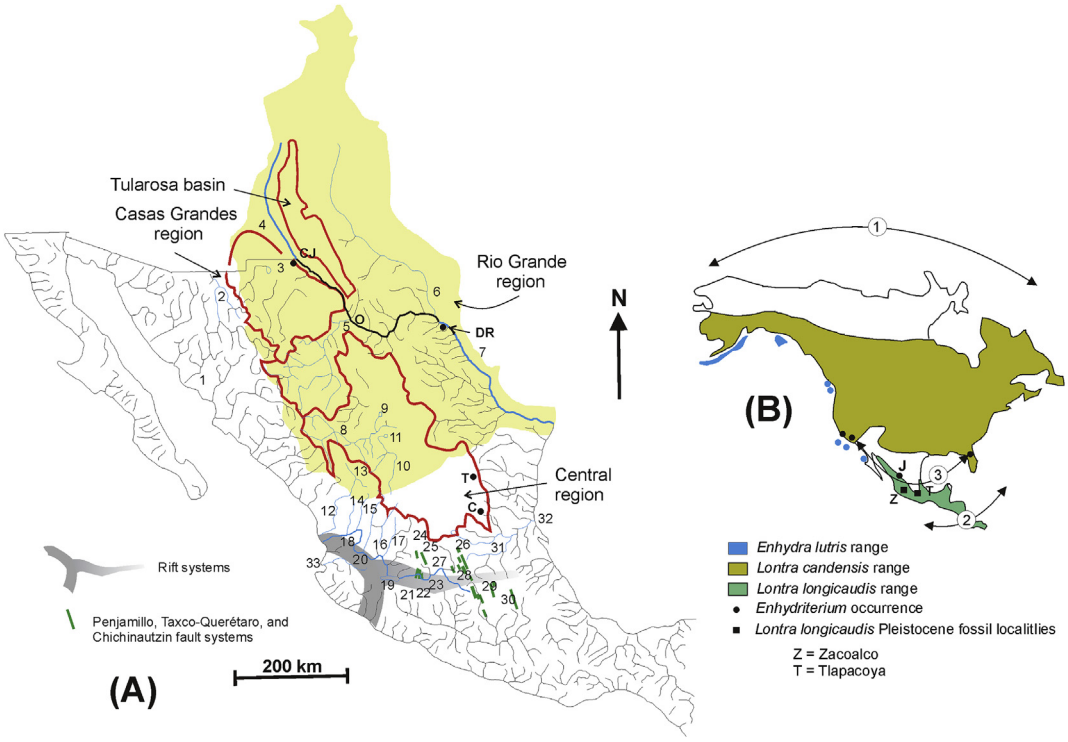

Fig. 1. A) Map showing Mexico's hydrography and the extent of the Rio Grande region (after Smith and Miller, 1986). Rivers and lakes mentioned in the text are: 1 = Yaqui, 2 = Bavispe, 3 = Guzmán lake, 4 = Upper Rio Grande, 5 = Conchos, 6 = Pecos, 7 = Lower Rio Grande, 8 = Nazas, 9 = Lake Tlahualilo, 10 = Aguanaval, 11 = Lake Mayrán, 12 = Mezquital, 13 = Tunal, 14 = Jesús María, 15 = Bolaños, 16 = Tlaltenango, 17 = Juchipila, 18 = Grande de Santiago, 19 Chapala lake, 20 = San Pedro Lagunillas lake, 21 = Zirahuén lake, 22 = Pátzcuaro lake, 23 = Cuitzeo lake, 24 = Lagos de Moreno, 25 = El Bajío, 26 = San Juan del Río, 27 = Lerma, 28 = Valle de México, 29 = Serdán Oriental, 30 = Tehuacán Valley, 31 = Moctezuma, 32 = Pánuco. Cities: C = Cárdenas, CJ = Ciudad Juárez, DR = Del Rio, O = Ojinaga, T = Tula. (B) The three hypothetical migration routes that otters may have used to cross the continent. It also show the sites where *E. terraenovae* have been found outside Mexico, as well as the localities where Pleistocene fossils of *L. longicaudis* have been reported (Modified after Tseng et al., 2017).

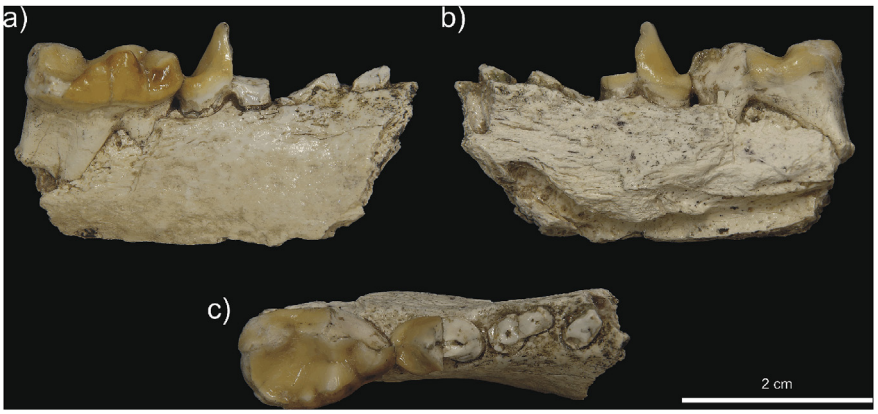

Fig. 2. a) Labial view, b) Lingual view, and c) Occlusal view of MPGJ 3586 *Enhydritherium terranovae*, which is a left mandibular ramus with m1, fragment of p4, p3-2 broken and alveolus of canine. Collected at locality Zac Juch 47 El Resbalón; early Hemphillian age (for a complete description see: Tseng et al., 2017).

importance of the fossil *E. terraenovae* found in Mexico resides in: (1) it is the southernmost fossil record of a late Miocene otter in North America so far known; (2) it is also the first fossil occurrence in a land-locked basin that is at a significant distance (ca. 200 km) from the coast and at a considerable elevation (presently ca. 1250 masl); (3) It confirms that *Enhydritherium* was capable of living in the late Miocene in a completely freshwater environment (previously reported *Enhydritherium* fossils are associated with marine vertebrates (Berta and Morgan, 1985) or in coastal regions in both nearshore marine and inland fresh water environments (Lambert, 1997); (4) the new fossil supports a possible over-land dispersal route through Mexico between the Pacific coast and Florida (Fig. 1B). Biochronologic age of the fossil occurrences in California and Florida ranges from early Hemphillian (6–7 Ma) to late Hemphillian (4.9–5.3 Ma) and the Zacatecas fossil age is between 5.59 and 6.95 Ma, as inferred from U-Pb ages obtained from zircons recovered from ash-fall beds above and below the fluvial sediments where the fossil was collected.

Based on the osteological study of an incomplete skeleton of *Enhydritherium terraenovae* found at Moss Acres Racetrack in Florida (Fig. 1B), Lambert (1997) concluded that this otter was a habitat generalist capable of living in both nearshore marine and in fresh water habitats. It also had locomotive capacity to move overland. Feeding habits of this otter included extremely hard food items (molluscs) and large fishes.

In this contribution we focus on the hypothesis of a migration route along riparian environments of *Enhydritherium terraenovae* from one ocean to the other through an unknown region of Mexico (Fig. 1B). Assuming, as demonstrated by the Juchipila fossil, that *E. terraenovae* successfully inhabited perennial river system up to an area close to its headwaters, the otters still had at least one more barrier to cross and get to the ocean on the opposite side of the continent. The most obvious barrier is the continental divide and, as it will be discussed in this paper, another possible obstacle could be the existence of large regions with endorheic drainages (i.e., internally drained basins), which are presently very extensive in central and northern Mexico (Fig. 3) and that, based on the geological history of Mexico, are likely to have existed at different times during the Neogene. We assumed that once the otters passed these topographic obstacles they started to colonize a river system that drained in the opposite direction. Here we propose that a viable process that facilitated this crossing is the phenomenon of river-rearrangement (Bishop, 1995), a common process that may be caused by climate forcing (Heller et al., 2011), tectonic activity (e.g. Sharman et al., 2017), volcanism (Repasch et al., 2017), sea level changes or a combination of several of these factors. To evaluate our

Fig. 3. The Great Divide of North America (Modified after Gonzalez, 2003). Large endorheic regions are also shown. There are three regions where the divide splits surrounding extensive areas with internal drainage. West of the divide is shown the outline of the Great Basin, another endorheic basin presently separated from the Great Divide.

hypothesis we assume that otters must have made the crossing some time during or prior to the late Miocene (ca. 7 Ma) and that habitat requirements of *Enhydritherium terraenovae* were very similar if not identical to those of *Lontra longicaudis*. We began our analysis examining what is known about present day hydrology of Mexico in the region between latitude 20°N and the Mexico-USA border. Fig. 1A shows a simplified hydrological map.

Additionally, we extend our analyses into the Cenozoic tectonic and climatic history of northern and central Mexico as major tectonic features, such as the thrust and fold belt of the Sierra Madre Oriental, the broad highland caused by volcanism of Sierra Madre Occidental, the endorheic basins bounded by block mountains of the Basin and Range and/or the Gulf of California Extensional Province, and volcanism of the Trans Mexican Volcanic Belt (Fig. 4) must have played important roles in the integration and disintegration of fluvial systems.

1.1. The continental divide in Mexico

The continental divide is a physiographic feature that "separates surface waters that ultimately flow to different oceans, …seas … or coastlines on different sides of a continent" (Gonzalez, 2003). The

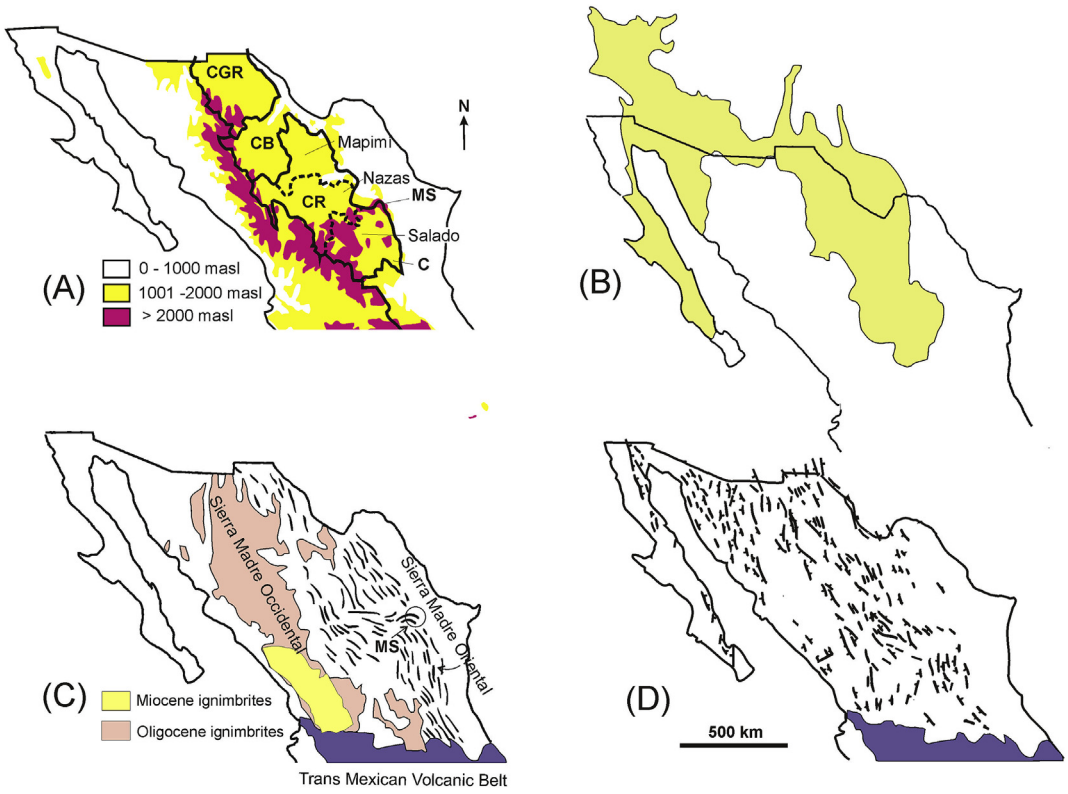

Fig. 4. A) Endorheic regions (INEGI, 2017) and hypsometry. Key to abbreviations CGR = Casas Grandes Region, CB = Conchos Basin, CR = Central Region, MS = Monterrey Salient, C = Cárdenas B) Distribution of *Larrea divaricata* as an indicator of the edge of North America deserts (Shreve, 1940, Rzedowski and Calderón de Rzedowski, 1988). This desert shrub is a good indicator of arid and semi-arid conditions in terrains where soils are rich in calcium. C) Major mountain ranges in central and northern Mexico (simplified after de Cserna, 1989 and Ferrari et al., 2007), D) General distribution of normal faults attributed to the southern Basin and Range (Henry and Aranda-Gómez, 1992). See text for discussion.

continental divide in Mexico is the southern extension of the Great Divide in the USA (Figs. 3 and 4A).

One of the most conspicuous features of present-day drainage system in northern and central Mexico is the existence of two vast regions occupied by a complex array of endorheic basins, which are separated by the Río Conchos basin (Fig. 1). We refer to these irregular-shaped zones, as the Casas Grandes and Central endorheic regions (Fig. 4A), avoiding the use of Mesa or Meseta Central as the term has been previously used with different meanings in the literature related to Mexico's physiography (Raisz, 1964; West, 1964), the evolution of the drainage systems (e.g., Miller and Smith, 1986; Domínguez-Domínguez et al., 2006; Dickinson, 2015) or the regional geology and tectonics of Mexico (e.g. Nieto-Samaniego et al., 2005). A small portion of the Casas Grandes region is located in southwestern New Mexico (Miller and Smith, 1986) and the late Cenozoic evolution of its surroundings areas is more closely related to the Gila river drainage system and to the opening of the Gulf of California (Dickinson, 2015). The southwestern boundary of the Tularosa endorheic basin (Fig. 1A) in New Mexico and Texas follows the trend of the Rio Grande and it appears that it used to be part of the Casas Grandes region prior to the encroachment by the Rio Grande in the Pliocene (Repasch et al., 2017).

The Central endorheic region (Fig. 4A) is slightly over 950 km long and it is up to 500 km wide; it has an irregular, but elongated shape that is roughly parallel to and has about the same length as the Gulf of California. The total surface of the Central region is close to 290,000 km^2, an area that can be divided by two major divides into the Mapimí, Nazas, and El Salado subregions (Fig. 4A). Significant changes in the average elevation and geologic setting of these subregions suggest that their evolution and origin might be different.

Taking into account the existence of the endorheic regions, it turns out that Great Divide in northern Mexico splits into two subparallel branches. As a general rule, the western branches of Casas Grandes and Central regions follow elevated terrain with altitude 2000 masl or higher and it is partially or completely covered by thick successions of Cenozoic volcanic rocks of the Sierra Madre Occidental (Fig. 4A and C). Thus, topography created by voluminous Cenozoic volcanic activity is a primary control in the location of the western divides. Areas near the western branch of the divide where the volcanic cover is not continuous occur in northeastern Sonora and in the region located immediately north of the Trans Mexican Volcanic Belt (Fig. 4C). In both areas tectonically-controlled valleys are partially filled with graben-fill sediments and block mountains are developed in the Cenozoic volcanic rocks. In the case of the Río Conchos basin, which separates the Casas Grandes and Central regions it appears that the local uplift that generated the portion of the divides that are roughly parallel to the Rio Grande was defeated by erosion and the transverse canyons where the Conchos river is entrenched, just SW of Ojinaga (Fig. 1), indicate that the gorges are either antecedent or superimposed (King and Adkins, 1946) in origin.

The eastern divide of the Central endorheic region follows the western boundary of the High Ranges of Sierra Madre Oriental as defined by Raisz (1964) and in most places its elevation tends to be lower than elevations on opposite sites on the western divide. A notable exception occurs at the Monterrey Salient (MS Figs. 1 and 4C), where the terrain is as high or higher than in the opposite western divide.

1.2. Evolution of drainage systems

Rivers initially follow the slope of the land surface and later may adjust to structure as they incise the terrain where they flow (Twidale, 2004). Drainage networks are products of the tectonic and climatic history of the regions where they occur, and dynamically respond to the ever-changing conditions. Major forcing factors in the evolution of drainage networks are tectonic activity, volcanism, climate, and sea level changes. Drainage rearrangement, via stream capture, beheading, or river diversion (Bishop, 1995) may occur even in tectonically quiescent settings (Prince et al., 2011) where they are caused by topographic asymmetry in the basin or by spatial patterns of precipitation caused by rain shadows along mountain ranges. Entrapment of sediments in endorheic basins caused by the reduced capacity of the river system to remove erosion products and isostatic response to differential rates of erosion, coupled with mild tectonic activity in nearby areas may be the cause of formation of extensive internally-drained regions such as the Great Divide Basin (Fig. 3) in the western part of the United States (Heller et al., 2011).

Drainage networks may act as a register of tectonic activity and climate change for long periods of time, despite the fact that present day drainage systems are profoundly affected by the most recent events (e.g. D'Agostino et al., 2001). Stephenson et al. (2014) have argued that it is possible to infer from the quantitative analysis of the present-day drainage network of Mexico and the southern USA information about their uplift history in the last 40 Ma. Inversion of longitudinal profiles of four Mexican rivers (Fuerte, Pánuco and two unspecified tributaries of the Grande de Santiago, Fig. 1) permit to infer in all of them an uplift event at the time span between 16 and 22 Ma at rates between 0.1 and 0.3 mm/yr and a younger event around 8–10 Ma recorded only in the tributaries of the Grande de Santiago (Bolaños and Jesús María rivers?). Stephenson et al. (2014, their Fig. 7) do not address the problem of the Casas Grandes and Central endorheic regions in their paper and assume that the vast region presently occupied by them is part of the Rio Grande drainage system in their modeling.

1.3. Processes involved in the formation of internally drained basins

The Casas Grandes and Central regions are wholly enclosed within the arid and semi-arid regions of central Mexico (Fig. 4B) as inferred by Shreve (1940) and by Rzedowski and Calderón de Rzedowski (1988) from the distribution of *Larrea divaricata* and within the eastern branch (Fig. 4D) of the southern end of the Basin and Range Province (Henry and Aranda-Gómez, 1992). Globally, endorheic basins form 20% of the emerged land surface and most of them are enclosed in arid regions, a fact that suggests that climate is an important factor in their formation. As a consequence of their low average run-off produced by arid environments and the fact that they act as sediment traps, internally drained basins commonly lack well-integrated drainage systems (e.g. the Nazas and Aguanaval river systems and the region near Ojinaga: Figs. 5 and 6). Water in endorheic basins converge into lakes, which in arid lands are ephemeral and may form salt flats or, in very dry regions, run-off may end by infiltration and evaporation in alluvial plains or alluvial fans (Dorsaz et al., 2013).

Endorheic basin formation and disintegration of a channel network are produced when a fluvial system is defeated by a topographic barrier created by tectonic uplift (Fig. 7) or by blockage by volcanic products. Frontal ranges in the foreland regions of contractional tectonic systems, coupled with low precipitation caused by rain shadows produced by them may form extensive endorheic basins that could last for long periods of time and grow as they coalesce as sediment overtops some of the divides (Sobel et al., 2003). The eastern boundary of the Central endorheic region, between the Monterrey Salient and Cárdenas (Fig. 4A and C) is seen by us as an example of this. Crustal extension and local associated uplift caused by isostatic response may form effective topographic barriers a few tens of kilometers away perpendicular to the strike of major normal faults systems (Fig. 7) and many tens of kilometers along their strike (King and Ellis, 1990). Obliteration of previous landscapes by intense volcanic activity and contemporaneous crustal extension may produce numerous internally drained basins that with time could merge when the intensity of both phenomena decrease (Spencer et al., 2008). Caldera-forming eruptions and emplacement of extensive wedge-shaped bodies of ash flow tuffs (e.g. Smith, 1960) may be especially effective in obliteration of drainage systems over broad areas in short periods of time (Manville, 2001) and distribution patterns of partially to densely welded ignimbrites in the formation of new, partially or completely reorganized fluvial systems. The highland where the western branches of the Great Divide in Mexico are located (Fig. 4A and C), are a clear example of the influence of volcanism in the regional hydrological patterns.

Major climate changes also have a pronounced effect on the drainage systems and may determine if work performed by rivers switch from aggradation to erosion or vice versa. An increase in aridity of the southwestern part of USA during the Miocene (ca. 12 Ma) reduced the stream flow and caused entrapment of sediments in internally drained basins, whereas intensification of the North American monsoon, a phenomenon that currently is responsible for 60% of the summer precipitation in northern Mexico (Mitchell et al., 2002) coincident with the opening of the Gulf of California (ca. 6 Ma) caused the modification of drainage networks and incision of basin fills. These large variations in climate were caused by major changes in circulation patterns in the oceans (Eronen et al., 2012), some of them driven by tectonic changes in remote regions (Chapin, 2008).

1.4. Biogeography of freshwater fishes, speciation and its timing

Among biologists who study the evolution and biogeography of endemic freshwater fishes in the southern part of the USA and northern and central Mexico there is a consensus that processes such as river network disruption, mainly through river capture or fragmentation (Dias et al., 2012), has played an important role in the evolution and speciation of these fishes (e.g. Meek, 1904; Albritton, 1958; Miller and Smith, 1986). However, a comparison of distribution of living fish species with fossil fish fauna and present-day major drainage systems in the area suggests that their distribution is more influenced by major, older tectonic features (Fig. 4), such as highlands produced by volcanism in the Sierra Madre Occidental or the Trans Mexican Volcanic Belt or by folds and thrust faults in the Sierra Madre Oriental, or location of major Basin and Range normal faults than by present day hydrology (Miller and Smith, 1986). Repeated events of watershed communication by river capture or of isolation of part of drainage system (Fig. 5) caused by formation of internally drained basins probably caused allopatric speciations of freshwater fishes in the region (Webb et al., 2004).

Meek (1904) established that of 11 freshwater fish species collected by him at Río Mezquital (Figs. 1 and 5), 8 belonged to the Rio Grande fauna. Based on this information, and supported by geologic reconnaissance work in the surroundings of Durango city, Albritton (1958) concluded that El Tunal river once formed part the Rio Grande hydrologic region (Fig. 1A), despite the fact that the Rio Grande and upper Mezquital drainages systems are now hundreds of kilometers apart, separated by the Central endorheic region. Currently, El Tunal river drains into de Gulf of California via the

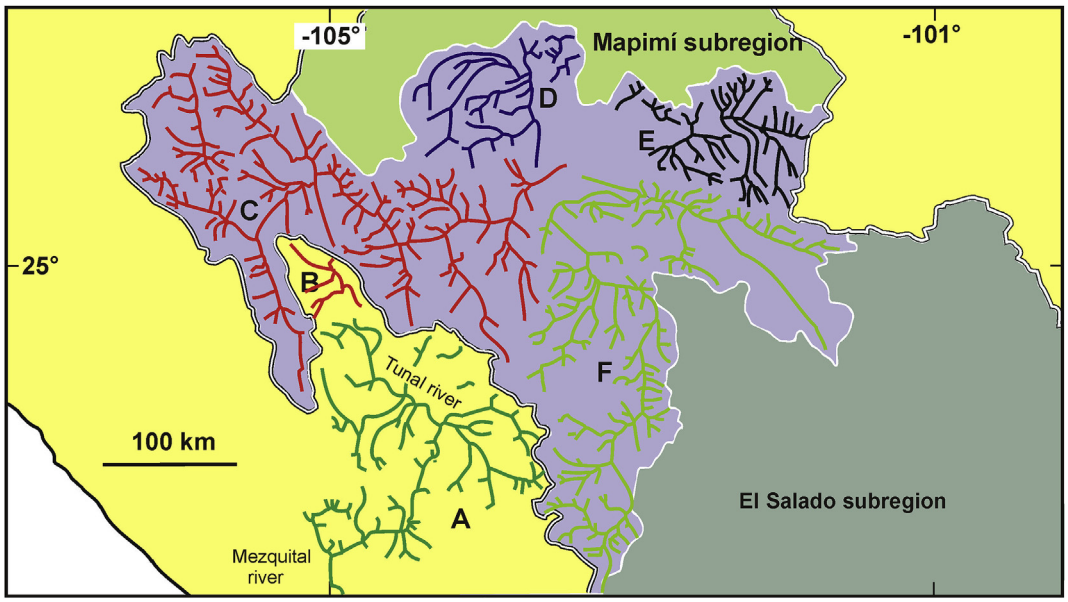

Fig. 5. A closer view of the drainage systems within the Nazas sub region. The Nazas (C), Aguanaval (F), and Laguna de Santiaguillo (B) river systems are examples of disintegration of drainages. All these rivers end at playa lakes. Southwest of these rivers is the headwaters of the Mezquital river system (A), where there is geomorphological and biogeographic evidence of capture of the Tunal river. Near the boundary between the Nazas and Mapimi sub regions, there are other isolated fluvial systems (D and E).

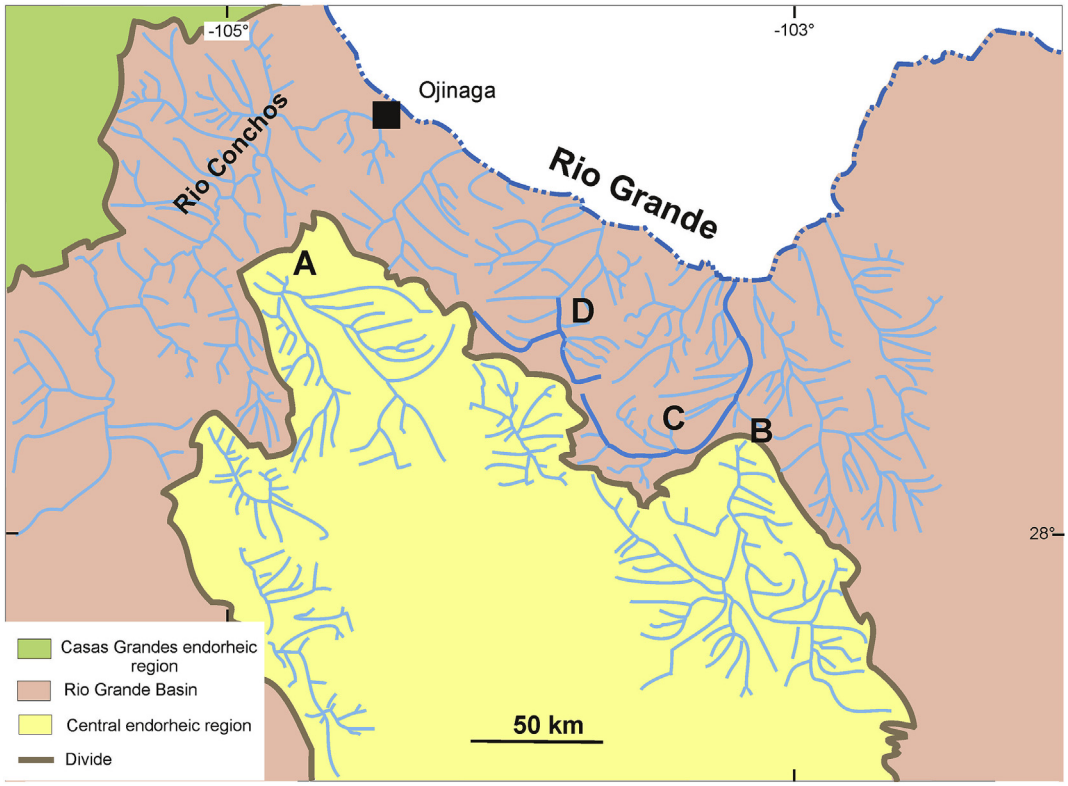

Fig. 6. Simplified hydrological map of the Ojinaga region. The northernmost and southeastern portions of Casas Grandes and Central endorheic regions are shown. Close to the divide there are two dendritic arrays (A and B) that were isolated from previous rivers that debouched into the Rio Grande. The divides are low and inconspicuous. C and D are fishhook and grapnel-shape arrays that are consistent with river captures.

Mezquital river (Fig. 1) and hydrographic maps show at their junction are several "fishhook" arrays (Figs. 5 and 8) that we interpret as elbows of capture (Lauder, 1968; Twidale, 2004). The capture of El Tunal by the Mezquital river occurred during middle Pleistocene (Albritton op. cit.), thus the inferred connection of El Tunal with rivers that may have drained into the Gulf of Mexico, via the Nazas and/or Aguanaval fluvial systems (Fig. 5), which presumably debouched into the Lower Rio Grande system (Fig. 1) is older. *Characodon* is found in the headwaters of El Mezquital river and in the Mayran lake fed by the Aguanaval river (Fig. 1).

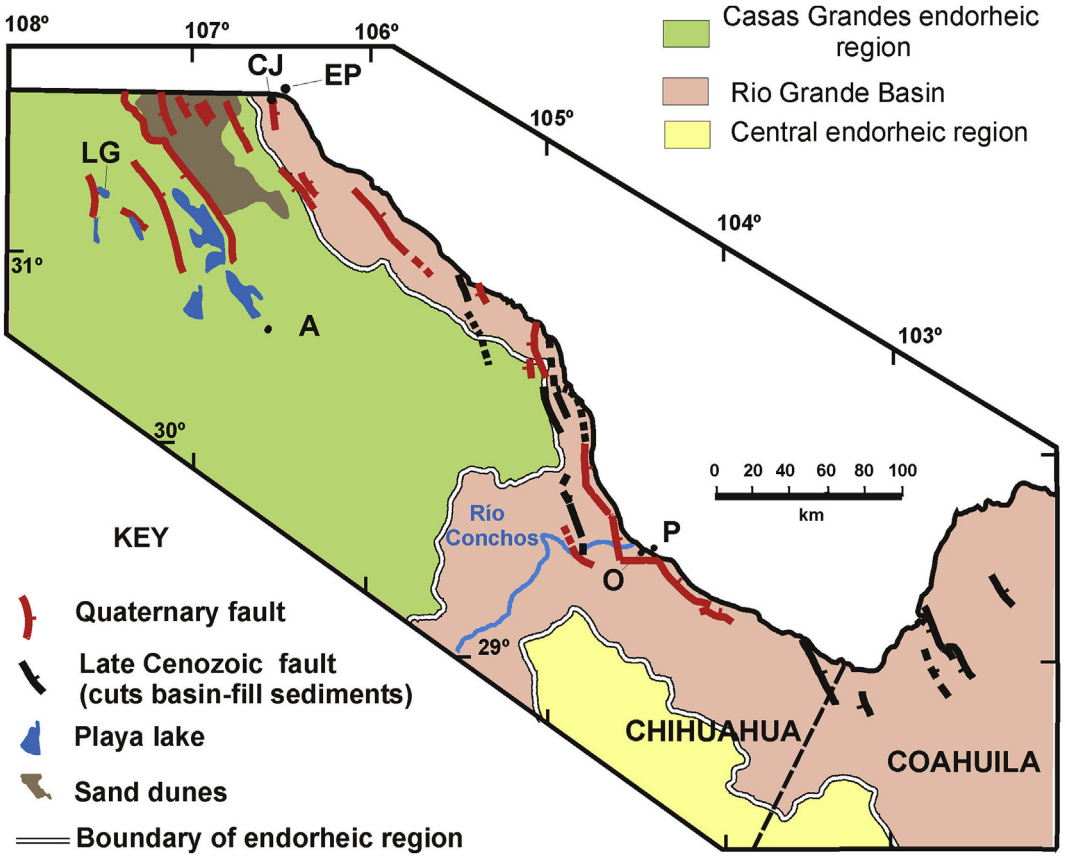

Fig. 7. Active faults near the Ojinaga region. These Quaternary normal faults are a short distance from and parallel to the northeastern divide of the Casas Grandes and Central regions. Key for abbreviations: A = Villa Ahumada, CJ = Ciudad Juárez, EP = El Paso, LG = Laguna Guzmán, O = Ojinaga, and P = Presidio.

Characodon diverged from the other goodeines approximately at 14.9 Ma (Webb et al., 2004)

Another example of the Rio Grande fish fauna inhabiting a river that now drains into de Gulf of California is the Río Yaqui (Fig. 1). In addition to these Atlantic versant freshwater fishes, the Río Yaqui and its tributaries the Bavispe and Papigochi rivers also host species of the Rio Colorado fauna (Meek, 1904) indicating complex changes in the late Cenozoic fluvial systems of southwestern USA and northern Mexico. A hydrographic map of the region near the western border of the Casas Grandes region also shows clear evidence of river captures (Suter, 2015) in the area between the headwaters of the Río Yaqui system and the endorheic basins (Fig. 9). Echelle (2008, p. 36) states "the divergence time estimates suggest … that the western pupfish clade became isolated from eastern pupfishes during the late Miocene to early Pliocene, and by middle late Pliocene these fishes were present in Death Valley, the Lower Colorado River, and Guzmán Basins". Western pupfish clad refers to those fishes inhabiting the Death Valley, Lower Colorado River and the Casas Grandes endorheic region, whereas the Eastern pupfishes are those of the Lower Rio Grande, the Old Río Nazas, and Río Conchos. Numerical estimates for the divergence events between Rio Grande and Guzmán faunas by Echelle (op.cit.) are between 5 and 6 Ma.

Smith and Miller (1986) in their Fig. 1 sketched what they considered the extent of the "Rio Grande region", a concept based on extant freshwater fish faunas, and include in it the two northern sub regions (Mapimí and Nazas, Fig. 4A) of the Central endorheic region, as well as the Río Conchos basin, the whole Casas Grandes region and the Tularosa endorheic basin of New Mexico and Texas (Fig. 1A). The southern boundary of their inferred Rio Grande region is close to the boundary between El Salado and Nazas regions shown in Fig. 4A. It must be stressed that "Rio Grande region" as defined by Smith and Miller based in its fish faunas (1986) has never been a single, well-integrated hydrographic system, as river systems in the area have experienced dramatic changes through the Neogene and Pleistocene. As an example of these changes, it must be considered that the Upper Rio Grande (Fig. 1) hydrographic system (i.e. from the headwaters of the river in Colorado to the Casas Grandes endorheic region) was largely controlled by the tectonic evolution of the Rio Grande rift during the Neogene and remained as a series of endorheic basins separated from the Lower Rio Grande (i.e. from Del Rio, Texas to the Gulf of Mexico coast: Fig. 1) until ~0.8 Ma ago (Repasch et al., 2017). Thus, the nearly linear (i.e. almost without important tributaries) and for the most part entrenched portion of the Rio Grande between El Paso and Del Rio was formed very recently. Likewise, the now endorheic basins of the Nazas and Aguanaval rivers (Fig. 1), that now end in the Tlahualilo and Mayran lakes (Fig. 1), respectively, probably drained in the past into the Lower Rio Grande (Smith and Miller, 1986).

Another important observation is that the fish faunas inhabiting in disjunct river systems within the endorheic regions of Mexico have species with sister groups both in the Rio Grande region and in the "Mesa Central region" as defined by West (1964) and used by Miller and Smith (1986), which is a region that encompasses the Trans Mexican Volcanic Belt (Fig. 4C), the area around Lagos de Moreno, El Bajío plain, and the Serdán Oriental and Tehuacán valley regions (Fig. 1A) in Puebla. Freshwater fish fauna in that broad and complex region is diverse and largely endemic. The diversity in the fauna is believed to result from allopatric speciation caused by a complicated history of drainage rearrangement and isolation

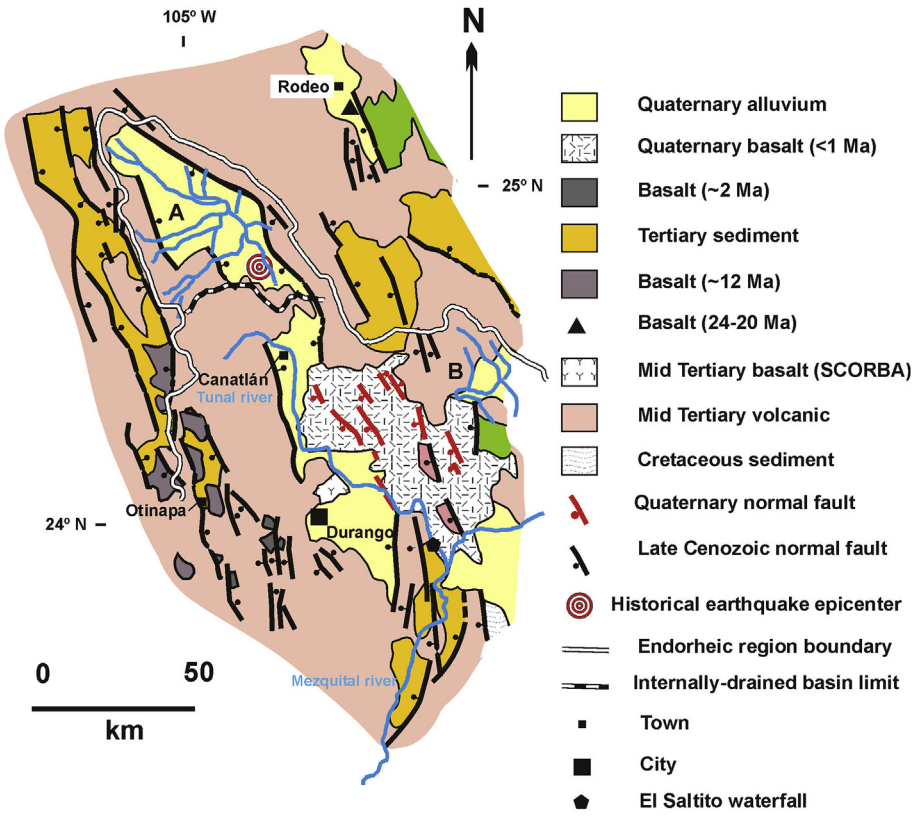

Fig. 8. Active faults and Quaternary volcanic field near the place where El Tunal river was captured by the Mezquital river (Modified after Aranda-Gómez, 1996). The location of El Saltito waterfall is also shown, as well as a small portion of the western branch of the Great Divide. The Santiaguillo basin is separated from El Tunal by a low, inconspicuous divide. A and B are examples of disintegrated drainages outside the Central Endorheic region.

during the Pliocene and Pleistocene, a time span when this area experienced intense volcanism (e.g. Gómez-Tuena, 2007; Ferrari et al., 2012) and normal faulting (e.g. Johnson and Harrison, 1990; Szynkaruk et al., 2004) along three sets of rift systems that joint in the Guadalajara triple junction (Fig. 1), and NNW-trending normal faults (Fig. 1A) that cross or intersect the fault systems of the Trans Mexican Volcanic Belt (Querétaro-Taxco and Pénjamo fault systems: Johnson and Harrison, 1990). The distribution of fishes of the genus *Chirostoma* throughout the Mesa Central (*sensu* West, 1964) a region that has, and has had many interior basins, demonstrates that the hydrology of the region has been continuously adjusting to changes caused by volcanic and fault activity. Former connections existed between the Lerma river system with closed basins such as the Valley of Mexico, Serdán Oriental, lakes Zirahuén, Pátzcuaro, Cuitzeo, and San Pedro Lagunillas (Fig. 1A). The same genus *Chirostoma* indicates a former connection with Laguna de Santiaguillo, just north of the site where the Tunal was captured by the Mezquital river (Figs. 1A, 5 and 8).

A potentially useful tool to understand the drainage system evolution is numerical age estimates (e.g. Doadrio and Domínguez-Domínguez, 2004; Webb et al., 2004; Echelle, 2008; Pérez-Rodríguez et al., 2009) based on mitochondrial DNA (mtDNA) nucleotide mutation rate and divergence time. However, these ages must be used with extreme care as sequence sampling choice and coverage (mtDNA vs. nDNA) may give very different results, sequence-change rate likely vary within and among taxa (Echelle, 2008), and additional variation with other factors such as temperature and body size of the fishes (Spencer et al., 2008). In addition to this, in order to calibrate the rate of mutation of the fishes, time constraints based on fossil records or on geological events assumed to be responsible for divergence (e.g. Albritton, 1958, Moncayo-Estrada et al., 2001) are also used. Thus, indiscriminate use of these ages to infer the numerical timing of geologic processes that caused river system rearrangements may result in circular reasoning, especially in a place like Mexico where detailed studies of the sedimentary successions accumulated in the continental fluvio-lacustrine basins are scarce or in many places non-existent, such as in the major endorheic regions, and knowledge of fossil fauna is also for the most part missing or just starting to develop (Guzmán, 2015). The fact that the valleys of the extensive endorheic regions still remain as aggradational systems also prevent their study as erosion has not exposed the sedimentary successions. Molecular divergence times of mtDNA lineages of Nazas, Conchos, and Rio Grande fishes of the genus *Pantosteus* are between 8.4 and 1.1 Ma (based on corrected fossil age estimates). However, the drainage changes that probably caused the divergence of *Pantosteus plebeius* (Río Conchos) and *Pantosteus nebuliferus* (Río Nazas) are still unknown (Unmack et al., 2014).

It has been suggested that hydrography of the Mesa Central *sensu* West (1964) is now in the process of being modified by rivers that drain into the Gulf of Mexico that have eroded through some portions of the fold and thrust belt of the Sierra Madre Oriental. Examples of this are the Moctezuma, San Juan del Río, Tamuín-Santa María rivers, all tributaries of the Río Pánuco (Fig. 1). Near the Pacific coast, rivers such as the Grande de Santiago and Ameca in the Pacific versant are also actively modifying the Lerma drainage system (Miller and Smith, 1986). Thus, it appears that the drainage systems of Mesa Central *sensu* West (1964) are being actively modified by rivers at the edges of elevated terrain.

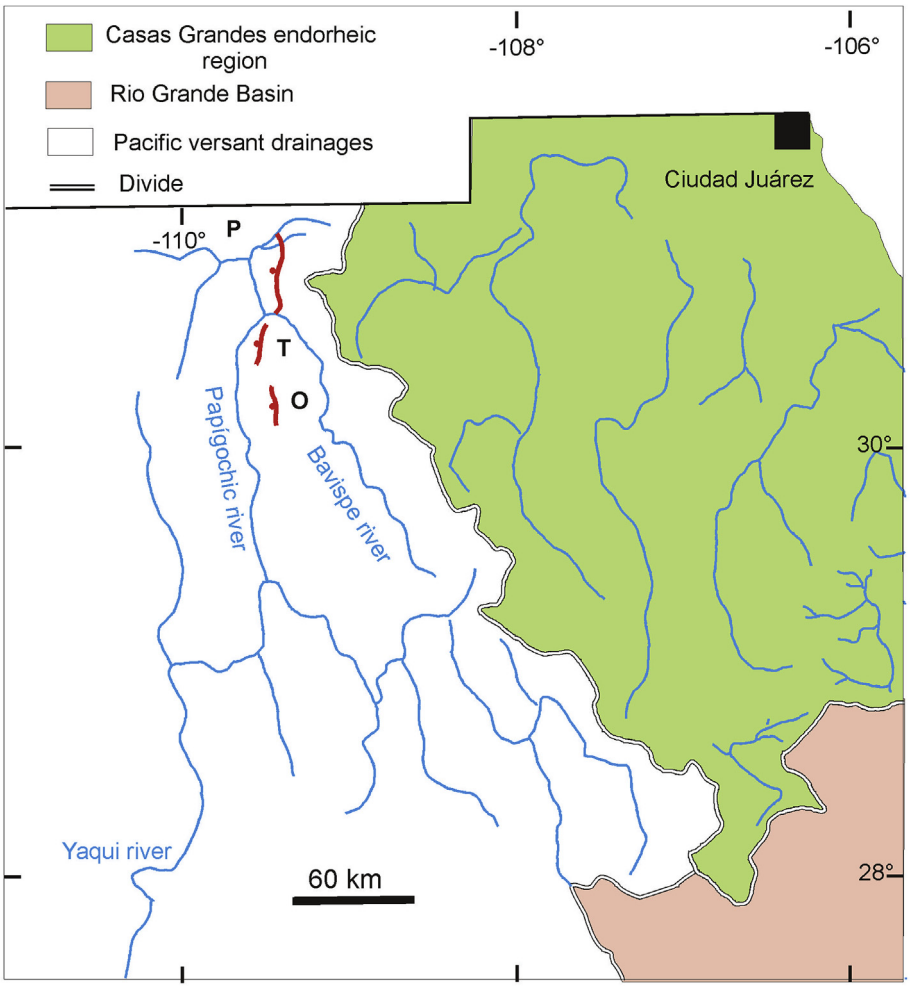

Fig. 9. Near the western divide of the Casas Grandes endorheic region there is evidence of several river captures by the Yaqui drainage system during the late Pliocene - early Pleistocene (e.g. Suter, 2015). The trace of the active Pitaycachi-Teras-Otates fault system and that of an older Neogene normal fault (Suter, 2008) is 15 km away from the divide and it is close to areas where transverse drainages between parallel, graben-controlled rivers, have been developed. Key for abbreviations: O = Otates, T = Teras, and P = Pitaycachi.

1.5. Some notes about the nature of the divides between the endorheic regions of Mexico and their surroundings

As far as we know, there is no published literature that specifically discusses the nature and probable origin of the divides that surround the endorheic regions in central and northern Mexico. In this section we briefly mention the geology of a few isolated areas located close to these divides where Quaternary tectonic activity has been reported in the literature. Following the work by Heller et al. (2011) in the Great Divide basin, we assumed that: 1) Plio-Pleistocene climate forcing played a major role in the formation of the closed basins as the endorheic regions are within the Chihuahuan desert (Fig. 4B), 2) their location is at least in part inherited from topography generated in previous tectonic events (Fig. 4C–D), and 3) the rain shadow effect of both major mountains, the Sierra Madre Oriental and Sierra Madre Occidental also cause low runoff within the closed basins favoring the entrapment of sediments within them. The question we want to address here is the possibility that, in addition to the three major factors enlisted, there is recent tectonic activity influencing the location of the divides. We succinctly review information on four areas: the Rio Grande basin between El Paso and the Big Bend (Fig. 7), the headwaters of the Yaqui river system (Fig. 9), and the Plio-Quaternary Camargo and Durango volcanic fields (Figs. 8 and 10), near the western boundary of the Central region. As it can be seen in Figs. 7–10 the common feature in all these areas is Quaternary normal faulting, with well documented structures a few tens of kilometers from the divides. In most cases the trends of the normal faults are roughly parallel to the divides. Thus, it appears that in some regions near portions of the extensive divides bounding the Casas Grandes and Central regions, isostatic rebound associated with normal faults contribute to their location.

2. Discussion

Based on the scant record of fossil otters and on the facts and inferences briefly reviewed in the previous sections, it appears that the goal of finding the probable route of migration of the otters across Mexico is very remote or impossible to reach at this moment. This is true in large part because the otter fossil records are very scant. It may be argued that the study of fossils of other species with more abundant fossil record (fishes, rodents, and other microvertebrates) through both time and space may help evaluate the hypothesis of otters crossing the continental divide thanks to the Mezquital river capture. However, we note that this goal may be impossible to reach as a large portion of the vast Central endorheic region is now formed by a series of disjointed drainages, which for the most part act as aggradational system where sediments are

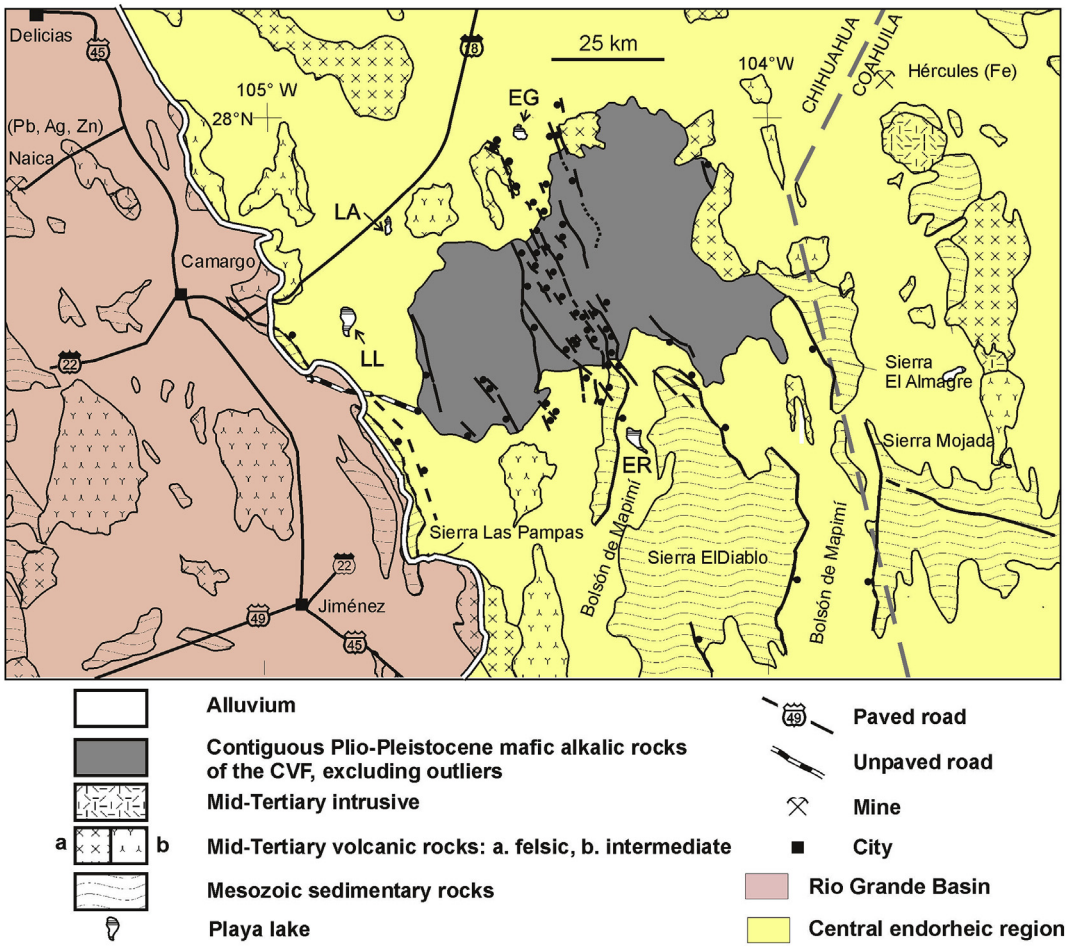

Fig. 10. The Plio-Pleistocene (4–0.09 Ma) Camargo Volcanic Field is crossed normal faults with inferred ages that range from 5 to 0.1 Ma. Age of faults in the central graben is ca. 2.0 Ma, based on isotopic ages (Modified after Aranda-Gómez et al., 2003). The divide between the Rio Grande Basin and the Central endorheic region lies ca. 40 km NE of the divide and the trend of late Cenozoic normal faults in the area is roughly parallel to the divide. Playa lakes: EG = El Gigante, ER = El Remolino, LA = Las Arenosas, and LL = El Llano.

trapped and erosion in the broad valleys is nil. This is a fact that may explain the lack of late Miocene – Pliocene vertebrate fossil localities between the Trans Mexican Volcanic and the southern portion of USA. Known Hemphillian and Blancan localities are situated at the fringes of the Central and Casas Grandes endorheic regions (Fig. 11), sometimes very close to the divide around them (e.g. the Yepómera and nearby localities).

Present day river systems in central and northern Mexico are almost certainly different from those in the late Miocene – early Pliocene. Divides on the eastern boundary of the Central endorheic region are mostly controlled by relict mountain ranges inherited from Hidalgoan Orogeny (Fig. 4C), which in northeastern Mexico ended in the late Eocene (Eguiluz de Antuñano, 2001; Chávez Cabello, 2005). The western limits of the Casas Grandes and Central regions closely follow high elevations produced by thick volcanic sequences formed during Sierra Madre Occidental volcanism, in the Eocene – Oligocene in northern Mexico and in the Eocene -Miocene farther south (Fig. 4C). The southern boundary of the Central region lies at variable distances north of the active Trans Mexican Volcanic Belt (Fig. 4C), where active volcanism and extension are present. Another factor that appears to be important in the formation of the vast endorheic regions are climate and structures related to Basin and Range extension (Fig. 4B and D). Desertification that began in the terminal Miocene event, between 7 and 5 Ma (Chapin, 2008; Herbert et al., 2016), and gradually intensified until reached its maximum in the Holocene (Miller and Smith, 1986) greatly contributed to the formation of the endorheic regions as a consequence of drastic reductions in runoff and river capacity of erosion within the central and southern part of the Chihuahuan desert (Fig. 4B). Formation of the Gulf of California at the end of the Miocene was also a major influence in the evolution of drainages, but it appears that its effects were different in the United States and Mexico. Whereas in the region around the Colorado Plateau played an important role in the creation of the Colorado and Gila river systems (Dickinson, 2015) and opening by drainage rearrangement of long-lasting extensive endorheic basins of the central part the Basin and Range Province (Sonder and Jones, 1999), in northern and central Mexico it appears to be a major factor in the integration of the Central endorheic region as a consequence of the intensification of the arid conditions. Another probable consequence of the formation of the Gulf of California in the river systems of Mexico was the increase of headwater erosion in the rivers along the western edge of the Sierra Madre Occidental, as the overall slope of the river systems increased due to reduction of the distance between the western branch of the continental divide (Fig. 4A) and the base level of rivers in the Pacific versant, now located in the Gulf of California. This reduction is at least equivalent to the average width (ca. 110 km) of the Baja peninsula and it is highly significant as the medial distance between the western branch of the divide is between 500 and 200 km. Locally,

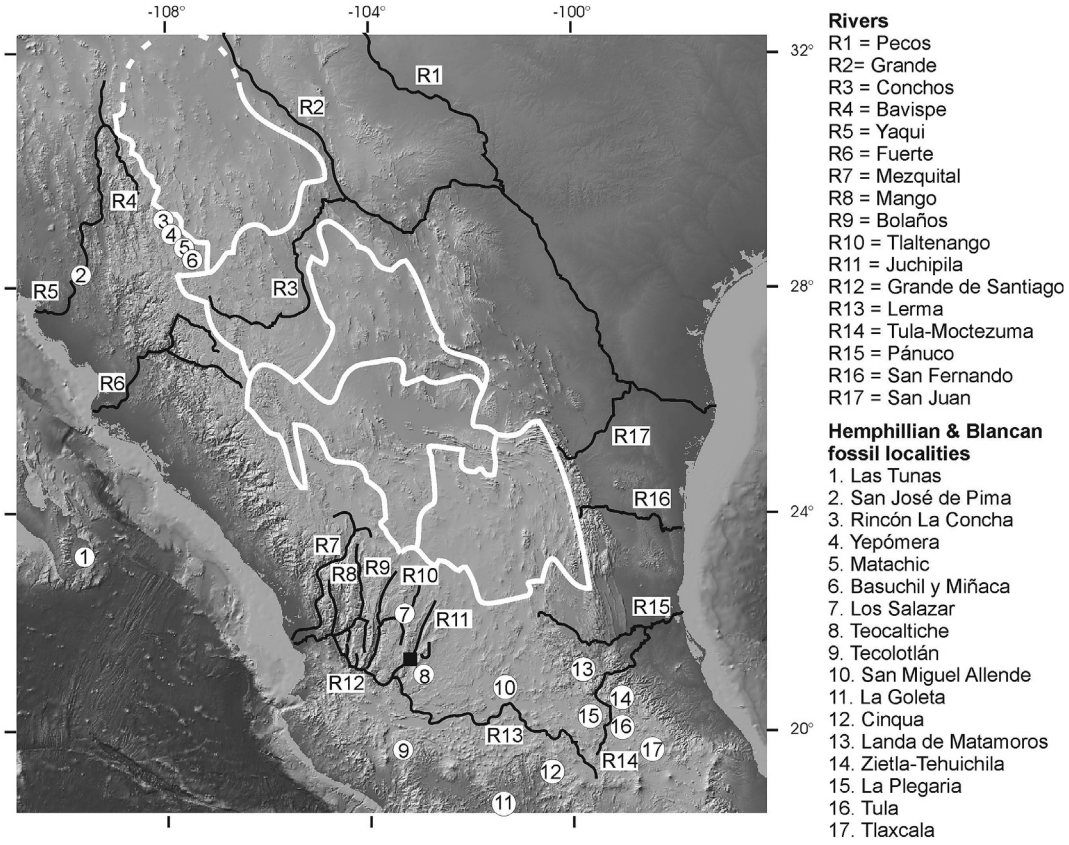

Fig. 11. Shaded relief map of central and northern Mexico showing: 1) present day major rivers (modified after: http://www.geomapapp.org), 2) the Central and Casas Grandes regions (white lines; dashed where location is approximate), and 3) Hemphillian and Blancan fossil localities (white circles) reported by Carranza-Castañeda (2006) and Montellano-Ballesteros and Jiménez-Hidalgo, 2006. The site where the *Enhydritherium terraenovae* fossil was found is shown as a black square labeled "J". Note that the Mezquital river follows a similar trend as the Mango, Bolaños, Tlaltenango, and Juchipila rivers, which drain into the Grande Santiago river. The Mezquital river debouch into the Pacific a short distance (ca. 14 km) from the place where the Grande de Santiago discharges into the ocean. Notice that within the endorheic areas major rivers are absent and topography is subdued with isolated mountain ranges separated by broad, alluvium-filled plains. Likewise, there is no Hemphillian and Blancan fossil localities in those areas.

river capture in the headwaters of river systems such as the Yaqui (Fig. 9) and Mezquital (Fig. 8) could have contributed to a local reduction of the extent of the Casas Grandes and Central endorheic regions, respectively. Even the capture of Lerma system by the Grande de Santiago near Chapala lake was probably influenced by the formation of the Gulf. We view present-day location of the western branch of the Great Divide in Mexico as a physiographic feature caused by a dynamic equilibrium between processes that favor the formation of endorheic basins and the erosive influence of the Gulf of California.

Despite the fact that it has been argued that eggs of some freshwater fishes may have experienced local transport from one watershed to another on the feet and/or feathers of aquatic birds (Echelle, 2008), biologists who investigate the biogeography of freshwater fishes believe that divergence events in their evolution are mostly tied to rearrangement of drainage systems by river capture or by fragmentation of watersheds by formation of endorheic basins. In this context it is worth mentioning that habitat fragmentation of freshwater fishes may also occur as a consequence of the formation of waterfalls (Dias et al., 2012) that may be related to differential erosion at the contact of rock units, faulting, and/or partial drainage blockage by volcanic activity. In the case of Mexico, there is at least a documented instance where a small waterfall separated two fish faunas (Domínguez-Domínguez et al., 2006). Populations of *Characodon lateralis* and *C. audax* are separated in the Tunal river by El Saltito waterfall (Fig. 8) and their inferred divergence age is 1.5 Ma.

The Juchipila river (Fig. 1) flows through a tectonic depression that is part of a set of NNE-trending conspicuous grabens in the southern end of the Sierra Madre Occidental. Scheubel et al. (1988) have regarded the drainage systems in this area as unusual as trunk rivers flow diagonally across the Sierra Madre Occidental into the Tepic-Zacolaco rift, instead of flowing transversely across it into the Gulf of California or the Pacific (Figs. 1 and 4C). Montgomery and López-Blanco (2003) analyzed the post-Oligocene history of incision in these rivers and documented captures driven by uplift caused by the Tepic-Zacolaco rift, a structure that controls the Grande de Santiago river. In our view, the trunk rivers studied by Montgomery and López-Blanco (2003), and the Mezquital river have roughly the same orientation and age (Ferrari et al., 2007 their Fig. 5) because they were formed by the same process, which caused the formation of an array of horsts and grabens in the area. Thus, this is an example of fluvial systems controlled by the structures.

López (1991) reported the occurrence of fossil fishes in lake sediments in the Juchipila basin, in the same sequence where the *Enhydritherium terraenovae* fossil was recently found. These fossil fishes were tentatively identified as Cyprinodontidae sp. by López (op. cit.) Our U-Pb data obtained in zircons recovered from ash-fall deposits interlayered with the fluvio-lacustrine sediments indicate that the succession where they occur is between 5.6 and 6.5 Ma (Carranza-Castañeda et al., 2013). Thus, a detailed study of these Cyprinodontidae sp. fossils in the Juchipila sedimentary succession and comparison with those found in other localities in the Rio

Grande region and in Mesa Central *sensu* West (1964) may shed some light about the evolution of drainage systems, help to estimate the age of formation of the endorheic regions, and probable route of migration of otters across the continent. Like the Mezquital river, present day Juchipila river drains into the Pacific and lies west of the Central endorheic region. Thus it seems fair to assume *Enhydritherium terraenovae* may have inhabited not only the Juchipila river, but was able to colonize all the rivers, included the Mezquital, in the NNE-trending grabens of the southern portion of the Sierra Madre Occidental (Fig. 11). Therefore, the otters may have crossed the continental divide near Durango city and reached the Gulf of Mexico via the Old Río Nazas – Aguanaval and Lower Rio Grande drainage systems. Currently, the Nazas – Aguanaval system is clearly disjointed as shown in Fig. 5. This hypothesis implies that the Mezquital capture must have occurred sometime during the late Miocene and not during the Pleistocene as proposed by Albritton (1958).

3. Conclusions

Otters probably crossed the continental divide aided by river piracy. Based on the location of the Juchipila fossil locality, the tectonic control on the location of the main rivers, the probability that otters may have colonized all the rivers in the grabens of the southern Sierra Madre Occidental, and the evidence of capture of the Mezquital river, it is hypothesized that they may have crossed the continental divide near Durango city (Fig. 10). This, together with the isotopic age constraints on the age *Enhydritherium terraenovae* fossil of Juchipila, implies that the Mezquital capture occurred during the late Miocene.

Alternative crossing routes suggested by present day hydrology might be the Grande de Santiago - Lerma and/or the Fuerte – Conchos – Lower Rio Grande systems (Fig. 11). However, the history of drainage systems in the Mesa Central sensu West (1964) and in the Trans-Mexican Volcanic Belt is very complex as a consequence of late Cenozoic volcanism and faulting, but evidence appears to exist in the biogeography of several fresh water fishes that many events of capture and isolation occurred in the Grande de Santiago -Lerma system. The Fuerte - Conchos - Lower Rio Grande is not regarded as a viable option as it is known that the Rio Grande segment between El Paso and Del Rio was established in the Pleistocene.

A general overview of a drainage map of central and northern Mexico generated with SIATL (INEGI, 2017) shows that there are two large endorheic regions. A comparison of the overall shape and the location of these regions with the hypsographic and tectonic maps and with a map of the arid and semi-arid regions in Mexico suggests that primary controls on their origin are the distribution of large mountain chains formed during the Cenozoic and current climate.

There is no systematic study of the extensive closed divides around the endorheic regions to ascertain their origin. Data compiled from the literature in areas near the divides suggest that in some places late Cenozoic tectonic activity may have contributed to their formation. Modest rates of extension coupled with marked influence of orographic shadows in the precipitation created subtle divides in many places.

The Central endorheic region is divided into three subregions by NE-SW or EW-trending secondary divides. It is remarkable that El Salado region is on average higher than both the Nazas and Mapimí regions, which broadly correspond with the Transverse Ranges of the Sierra Madre Oriental and with the Highland of Coahuila, respectively. Thus, it appears that the Mesa Central sensu Nieto-Samaniego et al. (2005) has experienced a period of uplift that remains to be documented.

The drainage systems of central and northern Mexico have not been studied in any detail and their evolution is practically unknown. By comparison with the evolution of neighboring drainage systems such as the Rio Grande, Gila and Colorado rivers in the southwestern part of the United States, it is safe to assume that they may broadly share some of their history as many of the major tectonic and climatic events affected both countries. However, there might be significant changes in the timing of the events, as deformation and volcanic pulses were diachronic. The Mesa Central sensu West (1964) certainly experienced tectonic and volcanic processes that can not be extrapolated to northern Mexico and the southern part of the United States as they are related to subduction along the Central America trench.

Acknowledgments

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